Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Roles of spatial scale in quantifying stock-recruitment relationships for American lobsters in the inshore Gulf of Maine

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0018.R1
Manuscript Type:	Article
Date Submitted by the Author:	27-Jul-2015
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Keyword:	spatial scale, stock-recruitment model, Bayesian, Homarus americanus, Gulf of Maine

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1 Roles of spatial scale in quantifying stock-recruitment relationships for American
2 lobsters in the inshore Gulf of Maine

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10 *Abstract*

11 It is well known in ecological studies that the choice of spatial scale can influence the
12 possibility of detecting ecological patterns and the type of patterns observed. However, this has
13 rarely been evaluated for fish stock-recruitment (SR) dynamics. Inappropriate scales may
14 result in failure to identify possible stock-recruitment relationships, especially for species with
15 complicated life history and stock structure and locally generated recruitment. Using American
16 lobster in the Gulf of Maine (GOM) as an example, we tested the hypotheses that the SR
17 relationship is detectable only at certain spatial scales and the functional SR relationships vary
18 with spatial scales. We estimated the SR relationship separately for American lobster in the
19 eastern and western GOM, which have strongly differing oceanographic conditions that may
20 result in different suitable spatial scale and SR dynamics for lobster. We analyzed data of 11
21 different spatial scales using a Bayesian method. The model fit and performances in the
22 posterior predictive assessment for the SR models were convexly related to the spatial scales.
23 The functional SR relationships differed for different spatial scale. The SR parameter estimates
24 are negatively or concavely related to the spatial scale. The best model was found at medium
25 spatial scale for both the eastern and western GOM and the scale differed between the eastern
26 and western GOM, suggesting that optimal spatial scale might be process-related. We
27 demonstrated that the choice of spatial scale directly affected the possibility of identifying the

28 SR relationship, the estimation of SR parameters, the type of SR relationships and the
29 predictive abilities of the SR models.

30 **Key words:** spatial scale, stock-recruitment model, Bayesian, *Homarus americanus*, Gulf of
31 Maine
32

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33 *Introduction*

34 Patterns and scales have long been recognized as two of the most important issues in ecological
35 studies (Levin 1992; Schneider 2001). Although often oversimplified, prevalent ways to make
36 data interpretations and predictions in ecological studies are often based on finding and
37 quantifying patterns in observed data. This results in a tendency to accept data at any spatial
38 scale as appropriate for testing a hypothesis, as long as the analysis is based on data with large
39 sample sizes and results in significant patterns (Rahbek 2005). However, mechanisms that
40 regulate patterns often operate nonlinearly at disparate spatial scales (Pineda et al. 2009).
41 Subject to such complexities, patterns may be different across scales of observations (Chase
42 and Leibold 2002; Rahbek 2005). It is also possible that patterns observed at one scale may not
43 be observable or predictive at other scales. The choice of spatial scale could alter the results of
44 any given analysis (Rahbek 2005). For this reason determining a suitable spatial scale is critical
45 in ecological studies.

46 The spatial scale effects include the extend, which refers to the boundary of the study area,
47 and the grain size, which refers to data resolution (Turner et al. 1989; Rahbek 2005).
48 Information would be lost if the spatial scale of data is too coarse (Turner et al. 1989;
49 Henderson-Sellers et al. 1985; Meentemeyer and Box 1987), whereas a too-fine spatial scale
50 may lead to large random noise and mask patterns in the data. Thus, the key is to analyze data at
51 an appropriate scale to reduce uncertainties in estimates, yet produce rich patterns that are

52 appropriate to the local ecological processes.

53 Spatial scale issues have been well recognized in studies of patterns of species richness

54 and diversity (Levin 1992; Schneider 2001; Chase and Liebold 2002; Rahbek 2005). For

55 example, the relationship between primary productivity and species diversity was

56 dome-shaped when data were analyzed at a local spatial scale with small grain sizes but

57 positively linear at a regional scale with large grain sizes (Chase and Leibold 2002).

58 Relationships between altitude and species richness vary with the length of the gradient

59 surveyed: dome-shaped relationships were most frequently observed when analyzing the data

60 at small local scales and the relationships disappeared at large regional scales (Rahbek 2005).

61 In marine ecosystems, the spatial scale issues have been considered in studies of population

62 connectivity and recruitment variability, which are important for understanding marine

63 population dynamics and ecosystem resilience (Caselle and Warner 1996; Myers et al. 1997;

64 Cowen et al. 2006; Steneck 2006; Xue et al. 2008; Incze et al. 2010). For example, Myers et al.

65 (1997) concluded that the spatial scale of recruitment correlations for marine species is

66 approximately 500km (11 fish species). Spatial scale of population connectivity is roughly 10

67 to 100 km depending on fish species (Cowen et al. 2006). However, these concepts have not

68 been incorporated into studies of fish stock-recruitment (SR) dynamics, which is critical in

69 fisheries management (Hilborn and Walters 1992).

70 Stock-recruitment relationships with or without linkages with environment are generally
71 difficult to quantify for marine populations (Hilborn and Walters 1992). Various factors,
72 including measurement and process errors, complex biological processes, highly varied
73 survival rates of pre-recruits, and non-stationary environment, tend to mask the relationships
74 (Hilborn and Walters 1992; Myers et al. 1996; Needle 2001). Moreover, factors such as pelagic
75 larval duration, larval behavior, adult spawning strategy, predation, food availability, and
76 circulation that regulate the recruitment dynamics often operate at differing spatial scales
77 (Cowen et al. 2006). The spatial scale suitable for estimating the SR relationship should be the
78 scale at which local recruitment can be self-sustained over the natural ranges of interactions of
79 all the biological and ecological processes. Thus, choices of spatial scale may influence the
80 possibility of detecting the SR patterns and the type of SR patterns observed.

81 American lobster support one of the most valuable fisheries in the USA with exvessel
82 revenues of \$401 million during 2010 (ASMFC 2009). At least 80% of commercial catch is
83 from inshore waters of the Gulf of Maine (GOM; ASMFC 2009). The landings consist largely
84 of lobster newly molted into the legal size, making it a recruitment fishery (ASMFC 2009). The
85 SR relationship for the American lobster is not well understood.

86 The American lobster has three planktonic larval stages and one planktonic post-larval
87 stage that is morphologically similar to the adult body form. The larvae stay in the water
88 column for roughly 15 to 20 days (ASMFC 1997). Several days after molting to the post-larval

89 stage, the postlarvae start to settle and become young-of-year (YOY) lobster (~10 mm carapace
90 length [CL]; Cobb et al. 1989). Juveniles and new fisheries recruits are mainly distributed
91 throughout the inshore waters (at depth < 50 m). After the juveniles become sexually mature
92 (around 60 mm CL), they tend to move towards deeper waters (Lawton and Lavalli 1995).
93 Different life history stages tend to have different ecological characteristics and habitat
94 requirements (Aiken and Waddy 1986; Fogarty and Idoine 1986; Mercaldo-Allen and Kuropat
95 1994; ASMFC 2009).

96 Processes that determine lobster recruitment dynamics, such as temperature, salinity,
97 substrates, predation, and food supplies, vary across life history stages that are found in
98 different habitats. The effect of these processes is likely to operate at different spatial scales.
99 Moreover, Xue et al. (2008) and Incze et al. (2010) indicated considerable potential that a
100 significant amount of lobster recruitment in the coastal GOM is derived from local sources.
101 Whether the recruitment is a local event or global phenomena could influence the possibility of
102 detecting the SR relationships at a stock level. Thus, the spatial scale of effective biological
103 processes may be critical in analyzing the SR relationships. However, this issue has not yet
104 been considered in estimating the lobster SR relationships.

105 The characteristics of complicated life history stages and locally generated recruitments
106 may be the reasons why only the relationships for adjacent or nearly adjacent life history stages
107 in relatively small regions were found for American lobsters. Positive relationships were found

for postlarvae and YOY lobster and between settlers and lobsters of nearly legal size (Incze et al. 1997; Wahle et al. 2004). Asymptotic relationships were found for the final larval stage and fishery recruitment in a relatively small region (Fogarty and Idoine 1986; Ennis and Fogarty 1997). No relationships have been identified across multiple life history stages and at the stock level over large geographic areas.

Mechanisms that regulate the SR relationship for American lobster may operate differently in different regions of the GOM because of the large differences in physical environment within the stock boundary. The GOM has a cyclonic flow of the interior regions and a coastal current system (Gulf of Maine Coastal Current; GMCC) over shallow coastal areas opposing the mean wind stress. The mean flow of GMCC is southwestward from Grand Manan Island to Massachusetts Bay, due to fresh-water inflows during the spring and summer (Brooks 1985). The GMCC creates strong northeast to southwest gradients in temperature, salinity, and productivity in the coastal GOM (Lynch et al. 1997; Pettigrew et al. 1998) and is prominent in the summer when larvae recruits are in the water column. The GMCC consists of 2 major branches: the Eastern Maine Coastal Current (EMCC) and the Western Maine Coastal Current (WMCC) (Fig. 1). The EMCC constitutes cold, deep, high-nutrient Labrador Current water and fresh water input from St John River and extends between Grand Manan Island and Penobscot Bay. It is generally the most consistent and vigorous part of the GMCC (Xue et al. 2008). The EMCC bifurcates in the vicinity of Penobscot Bay where a portion moves offshore

to the centre of the Gulf and the rest continues along the coast and combines with the outflow from Maine rivers (including the Kennebec, Androscoggin, Penobscot, Merrimack and St John rivers) to constitute the WMCC (Pettigrew et al. 2005).

The degree of continuity of EMCC to WMCC varies dramatically each year (Pettigrew et al. 2005), likely a result of differing strength of convective mixing in the winter and wind forcing (Xue et al. 2008). The freshwater plume that strengthens the southwestward flow also varies with a tendency to increase in recent years (2003 to 2010) compared to the years 1998 to 2002 (Churchill et al. 2005; McManus et al. 2014). The combination of the two sources of variation causes the WMCC to be highly variable. Manning et al. (2009) summarized the data of 227 satellite-tracked drifters deployed in the GOM during spring and summer from 1988 to 2007 and found that the EMCC is a relatively steady, flow-through system, while WMCC has more variable branching pathways. Circulation has strong influences on the distribution of lobster recruitment, at least for the first 3 planktonic stages (Xue et al. 2008; Incze et al. 2010).

Due to large differences in the EMCC and WMCC, the effects of circulation on the SR relationship should be operated at different spatial scales for the eastern and western GOM.

We tested the following three hypotheses: (1) the SR relationship for American lobster in the GOM is detectable only at certain spatial scales; (2) the functional SR relationships vary with spatial scales; and (3) the results in (1) and (2) are different because the mechanisms that regulate recruitment dynamics differ between the eastern and western GOM. To test our

146 hypotheses, we first quantify the SR relationships for the American lobster in the GOM using
147 different spatial scales of data. We then evaluate the performance of the models of different
148 spatial scales and the potential effects of misuse of spatial scale in predicting lobster
149 recruitment, particularly under low and high recruitment situations. The analyses are done
150 separately for the eastern (lobster management zones A to C) and western GOM (lobster
151 management zones D to G and the coastal New Hampshire area) where the coastal currents are
152 different in this magnitude and consistency (Fig. 1). We then discuss the role of spatial scale in
153 estimating the SR relationship for American lobster in the GOM.

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154 *Material and Methods*

155 *Data*

156 Recruitment is defined as density of young of year (YOY) lobsters during the settlement season
157 in the late summer to early fall. The recruitment data are collected by a settlement survey
158 conducted by Bigelow Laboratory for Ocean Sciences (years 2002 to 2005) and Maine DMR
159 (years 2005 to 2008). The YOY lobsters are collected by a suction sampler in cobble-boulder
160 lobster nursery habitats at fixed stations along the coastal northeast United States and Atlantic
161 Canada (Wahle and Incze 1997; Wahle et al. 2004; Wahle et al. 2013). Number, size and sex of
162 YOY and juveniles lobsters are recorded during the survey and the average density per m² is
163 estimated for each sampled location. Recruitment data are available for the seven lobster
164 management zones including 42 sites in the coastal Maine area (Fig. 2).

165 Spawning stock size is defined as the number of female lobsters measured in the fall
166 (October to December) with CL >60 mm, which is the minimum size at maturity for the GOM
167 stock (ASMFC 2009). The mean spawning stock size for each year and location where
168 recruitment data were collected was predicted using a two-stage GAM model which was
169 developed by Chang et al. 2010 using data collected by the Maine DMR inshore trawl survey
170 program from 2000 to 2006. A detailed description of the survey and model development can
171 be found in Chang et al. (2010). Eight environmental and spatial variables were considered in
172 the GAM model including temperature, salinity, latitude, longitude, depth, distance offshore,

and two sediment-related variables. The bottom temperature and salinity used for model prediction were obtained from the GoMOOS circulation nowcast/forecast system (Xue et al. 2005). The spawning stock sizes were estimated at 11 different spatial scales: 0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 32, 64, and 128 km grid diameter (a geometric series with a common ratio of 2). The estimates of spawning stock size for small spatial scales preserved local information, whereas the estimates of large spatial scales represented the mean condition of the whole study area. Examples of spatial distribution of the estimated spawning stock size and surveyed recruitment data are in Fig. 2. We analyzed the SR data from 2002 to 2008 for the eastern and western GOM (Fig. 2). Eleven different spatial scales and two different regions result in 22 sets of SR data being analyzed.

Model development

The Beverton-Holt (Beverton and Holt 1957) (B-H) and Ricker model (Ricker, 1954) with multiplicative lognormal errors were used to estimate the SR relationship for the 11 data sets grouped by different spatial scales for each region. The B-H model can be written as

$$R_{t,g} = \frac{S_{t,g}}{\alpha + \beta S_{t,g}} e^{\varepsilon_{t,g}} \quad (1),$$

where $R_{t,g}$ is the recruitment at time t grid g , $S_{t,g}$ is the spawning stock size that generate the recruitment measured at time t grid g , α determines the steepness at origin and β determines asymptotic limits ($1/\beta$) of the curve (recruitment reaches the asymptotic limits faster when β is smaller), and $\varepsilon_{t,g}$ are the random errors that followed $N(0, \sigma^2)$. The B-H

model assumes that density dependent mortality rate is related to cohort size and therefore it

appears an asymptotic-shaped curve. The Ricker model can be written as

$$R_{t,g} = \alpha S_{t,g} e^{-\beta S_{t,g} + \varepsilon_{t,g}} \quad (2),$$

where α determines the recruits per spawner when S is low and β determines the rate of

decrease of recruits per spawner as S increases. The density dependent mortality rate of the

Ricker model is assumed to be related to total stock size and therefore the Ricker model

exhibits a decline in recruitment levels at higher spawning stock size.

When the spatial scale used to group the spawning stock size is large enough, repeated

recruitment measurements occurred within the grids (Fig. 2). We included a random effect in

both equations 1 and 2 to account for the variation of the repeated measurements

$$R_{t,g,i} = \frac{S_{t,g,i}}{\alpha + \beta S_{t,g,i}} e^{\nu_{t,g} + \varepsilon_{t,g,i}} \quad (3)$$

$$R_{t,g,i} = \alpha S_{t,g,i} e^{-\beta S_{t,g,i} + \nu_{t,g} + \varepsilon_{t,g,i}} \quad (4),$$

where $\nu_{t,g}$ is the random effect at time t grid g and $\varepsilon_{t,g,i}$ is the individual-specific error and

both $\nu_{t,g}$ and $\varepsilon_{t,g,i}$ follows normal distribution. We estimated the parameters from the log

form of equations 1-4.

We used Bayesian method to estimate the SR relationship because it is a methodology for

capturing variability and risks resulting from the uncertainties inherent to a fishery (Punt and

Hilborn 1997). The models were run with 20,000 burn-in iterations, followed by 100,000

iterations for each of the three Markov chains. The sequences were thinned by keeping every

100th iteration to draw quasi-independent samples from the autocorrelated chains and form the posterior distribution for each parameter. A total of 3,000 samples were drawn for each dataset. Convergence of the parameters was examined using a potential scale reduction factor $\hat{R}_f$, which is used to indicate possible reduction of variance parameter of posterior distribution if the simulations continued (Gelman et al. 2004),

$$\hat{R}_f = \sqrt{\frac{\text{var}(\psi | R)}{W}} \quad (5),$$

where $\text{var}(\psi | R) = \frac{n-1}{n}W + \frac{B}{n}$, W is the within-sequence variance, B is the between-sequence variance, n is the sample size for each sequence (after discarding the first half of the simulations), and $\text{var}(\psi | R)$ is the marginal posterior variance of the estimate. The within-sequence variance should be smaller than the marginal posterior variance because the individual sequence covers only part of the target distribution. If the sequences are stable enough (converged), the two variances should be similar and the factor should be around 1. Parameter estimation was considered to be converged if its $\hat{R}$ value is close to 1 and below 1.1 (Gelman et al. 2004). The models were executed in WinBUGS 1.4.3 (Lunn et al. 2000) and convergence evaluations were carried out in R 3.0.2 (R Core Team 2013).

Prior distribution

The subjective choice of prior distributions receives one of the biggest criticisms for using Bayesian approach (Michielsens and McAllister 2004), although this could be an advantage when expert knowledge and information of the parameters are available. In order to be fair in

comparing data sets of different scales, we assumed noninformative prior distributions for all the SR parameters to make sure that the amount of information each data set received was approximately the same. An intuitive form of noninformative prior distribution might be a uniform distribution for which the parameter is estimated within a range of values with equal probabilities being selected. However, model parameterization determines whether the uniform prior distribution is truly noninformative. Jeffrey's prior, on the other hand, is a type of noninformative prior that is derived using Fisher information (square root of the determinant of the information matrix) and thus is invariant under parameterization choices (Robert et al. 2009). The Jeffrey's priors for standard Ricker and Beverton-Holt models were derived by Millar (2002) and were used in this study. The Jeffrey's prior for the Ricker model is

$$\pi(\alpha, \beta) \propto \frac{1}{\alpha}, \alpha > 0, \beta \geq 0 \tag{6}$$

and for the Beverton-Holt model is

$$\pi(\alpha, \beta) \propto \frac{\text{sd}(y(\beta))}{\alpha}, \alpha > 0, \beta \geq 0 \tag{7},$$

where $y_i(\beta) = \frac{S_i}{1 + \beta S_i}, i = 1 \dots n$ (8)

and $\text{sd}(y(\beta))$ is the standard deviation of the $y_i(\beta)$. For the variance parameter of the random effects $V_{t,g}$, we used the uniform prior density as suggested by Gelman (2006). Since we have enough data for both east ($n=84$) and west region ($n=187$), we should be able to estimate the variance of $\varepsilon_{t,g,i}$ with any reasonable noninformative prior distribution (Gelman 2006). We chose the uniform prior density for the variance parameter of the $\varepsilon_{t,g,i}$.

249 *Model evaluation and validation*

250 The following three methods can be used to evaluate Bayesian models (Gelman et al. 1996): (1)
251 evaluating sensitivity of prior distributions; (2) checking how well the model fits, and (3)
252 evaluating whether posterior inferences are reasonable.

253 We conducted sensitivity analysis to evaluate the influence of prior distributions on the
254 posteriors by assuming uniform priors with large upper bounds for parameters α and β , and
255 half-Cauchy priors for the variance of ν and ε . We changed prior distribution for one
256 parameter each time. We compared the results of posterior predictive assessment of these
257 models estimated using different priors to evaluate the sensitivity of prior distributions.

258 The goodness-of-fit for different types of SR models and models constructed using data of
259 different spatial scales was evaluated using model deviance:

$$260 \quad D(\theta) = -2 \log(L(R | \alpha, \beta)) \quad (9)$$

261 where $L(R | \alpha, \beta)$ is the likelihood function. The deviance was calculated for each iteration. A
262 lower deviance value indicates a better model fit.

263 Checking the posterior inference is crucial to Bayesian statistical analysis because the
264 analysis is conditional on the whole probability model (priors and likelihood functions). This
265 can lead to biased or unrealistic results when the model is far from plausible (Meng 1994;
266 Gelman et al. 1996). We checked the posterior inferences by comparing data simulated from
267 the posterior predictive distribution and observed data and evaluating whether the model can

replicate the observed data with reasonable probabilities (Gelman et al. 1996). The posterior predictive distribution is denoted as

$$p(R^{rep}|R, SR) = \int \int p(R^{rep}|\alpha, \beta, SR)p(\alpha, \beta|R, SR)d(\alpha)d(\beta) \quad (10),$$

where SR is the stock-recruitment model, R^{rep} is the replicated data that could have been observed if we redo the survey during the time period and location that R was observed, based on the current model assumptions and the parameter estimates. The simulation of R^{rep} started with drawing a set of parameters α_J and β_J , $J=1, \dots, N$, from the posterior distribution. In this study we drew 1,000 pairs of parameters from the posterior distribution. Given the parameter sets, we drew a simulated set of replicated data R_J^{rep} from the sampling distribution $p(R_J^{rep}|\alpha_J, \beta_J, SR)$. The observed data R and the replicated data R^{rep} are independent datasets and both represent possible datasets resulting from the given values of α and β and the SR model. A large or systematic difference between R and R^{rep} could be an indication of potential model failure.

The comparison of R and R^{rep} was carried out by a discrepancy measure, which is a sum of squares of standardized residuals of data with respect to their estimated expectations and variances, calculated for both observed and replicated datasets

$$D(R, \alpha_J, \beta_J) = \sum_{j=1}^n \frac{(R_j - E(R|\alpha_J, \beta_J))^2}{\text{var}(R|\alpha_J, \beta_J)} \quad (11)$$

$$D(R_J^{rep}, \alpha_J, \beta_J) = \sum_{j=1}^n \frac{(R_j^{rep} - E(R|\alpha_J, \beta_J))^2}{\text{var}(R|\alpha_J, \beta_J)}, \quad J=1 \dots N \quad (12),$$

where n is the sample size for each dataset and N is the number of parameter draws from the posterior distribution. The more overlap between marginal posterior distributions of the observed and predicted discrepancy measures, the better the model could replicate the observed data. We used overlap coefficient, defined below, to measure the overlap between the two marginal posterior distributions

$$\text{overlap coefficient} = \frac{D(R, \alpha, \beta) \cap D(R^{rep}, \alpha, \beta)}{\min(D(R, \alpha, \beta), D(R^{rep}, \alpha, \beta))}$$

The overlap coefficient is between 0 and 1 depending on the degree of overlapping, and it is 1 if the two distributions are completely overlapped and 0 otherwise.

The discrepancy measure is analogous to the classical goodness-of-fit measures. If the observed data follow normal distribution or are approximately normal, given α and β the discrepancy measure has a (or an approximate) χ_n^2 distribution. A classical p-value based on

D can be calculated as

$$p_c = \int \int p(\chi_n^2 \geq D(R, \alpha, \beta)) p(\alpha, \beta | R, SR) d(\alpha) d(\beta) \quad (13)$$

$$p_c^{rep} = \int \int p(\chi_n^2 \geq D(R^{rep}, \alpha, \beta)) p(\alpha, \beta | R, SR) d(\alpha) d(\beta) \quad (14),$$

where χ_n^2 is the chi-squared random variable with n degree of freedom. However, given the complexity of our models, the degree of freedom for the chi-square distribution is hard to estimate. Rather than assuming a χ^2 distribution and calculating the classical p-values, we used the Monte Carlo simulations to compute a Bayesian p-value (without any distributional assumption), which is defined as the probability that the replicated data are more extreme than

the observed data given the posterior distribution of α , β and the posterior predictive distribution of R^{rep}

$$p_B = \int \int \int I_{D(R^{rep}, \alpha, \beta) \geq D(R, \alpha, \beta)} p(R^{rep} | \alpha, \beta, SR) p(\alpha, \beta | R, SR) d(R^{rep}) d(\alpha) d(\beta) \quad (15),$$

where I is the indicator function. If the model can replicate the observed data well, the estimated Bayesian p-value should be close to 0.5.

We specifically examined potential implications of SR models of different spatial scales on predicting low (≤ 25 th percentile) and high (≥ 75 th percentile) recruitment since these are most important to fishery stock assessments. This is evaluated by comparing deviances summing over only the low and high recruitment

$$D_{25}(R_J, \alpha_J, \beta_J) = \sum_{j=1}^{n-k} \frac{(R_{(j)} - E(R | \alpha_J, \beta_J))^2}{\text{var}(R | \alpha_J, \beta_J)} \quad (16)$$

$$D_{75}(R_J, \alpha_J, \beta_J) = \sum_{j=k}^n \frac{(R_{(j)} - E(R | \alpha_J, \beta_J))^2}{\text{var}(R | \alpha_J, \beta_J)}, \quad J=1 \dots N \quad (17),$$

where k is the number of samples that exceed the 25th percentile or below 75th percentile.

317 **Results**

318 **Parameter estimates**

319 The $\hat{R}_f$ for the α and β parameters of the Ricker and B-H models for the 22 data sets
320 grouped in different spatial scales to mimic observing SSB and recruitment in different spatial
321 scales ranged from 1 to 1.09, suggesting that all the parameters estimates were converged
322 (Table 1).

323 The estimated parameters are not random across different spatial scales used to aggregate
324 the data (Fig. 3; Table 1). For the B-H model, the parameter estimates decreased with
325 increasing spatial scales (Fig. 3; Table 1). For the Ricker model, the parameter estimates are
326 concavely related to spatial scale (Fig. 3; Table 1).

327 **Model fitting**

328 The model deviances varied non-randomly with models constructed using data of different
329 spatial scales for both Ricker and B-H models and the two regions (Fig. 4). For the models
330 developed based on data of small spatial scales for both regions, the deviances were relatively
331 high, suggesting a poor model fit (Fig. 4). Model deviances started to decrease with spatial
332 scales after spatial scales reached 4 km for the eastern GOM and 2 km for the western GOM
333 with large variations (Fig. 4). The best model fit (i.e., model with the lowest deviance) was
334 found at the spatial scale of 8 km and 2 km for the eastern and western GOM, respectively,
335 indicating the existence of optimal spatial scale for data analysis (of all the spatial scales tested;

Fig. 4). The variance of the deviance at the optimal spatial scales were larger compared to the other spatial scale scenarios for both the regions (Fig. 4). After exceeding the optimal spatial scale, model fitting deteriorated suddenly for the eastern region. For the west region, model fitting deteriorated gradually after spatial scale of 32 km (Fig. 4). The range of spatial scales with low deviances (i.e., good goodness-of-fit) was from 2 km to 128 km for the western GOM, which is much wider than the eastern GOM where the low deviances only occurred at spatial scales of 4km and 8km (Fig. 4). The existence of the trend of model fits with respect to spatial scale supports our hypotheses (1) and (3) outlined early.

The performance of the B-H model was superior to the Ricker model at smaller spatial scales for both the regions (Fig. 4). When the spatial scale was larger than 4 km for the eastern GOM and 16 km for the western GOM, the Ricker model fit consistently had a better fit than the B-H model except for the spatial scale of 16 km for the eastern GOM model (Fig. 4). At optimal spatial scales, Ricker model was a better model for both the regions (Fig. 4). These results suggest that the choice of spatial scale could influence the type of SR relationship being observed. This result supports our hypotheses (2) and (3). The regional difference in the hypothesis (2) was less obvious than that in the hypothesis (3).

Model predictive assessment

The observed data were compared to the data simulated from the posterior predictive distributions. The Bayesian p-values and the marginal posterior distributions for different

levels of recruitment were presented in Fig. 5 and Table 2. The predictive assessment results showed that if all levels of the predicted recruitments were evaluated simultaneously, all the models could replicate the observed data well (overlap coefficient close to 1 and Bayesian p-value close to 0.5) except for the Ricker model based on data of 0.125 km spatial scale for the western GOM (Fig. 5; Table 2).

However, when the model performances were evaluated by levels of recruitment, the model performances were different by spatial scales, regions, and model types. The recruitments lower than 25th percentile and higher than 75th percentile were better replicated by the eastern GOM models compared to the western GOM models and for the Ricker models compared to the B-H models (Fig. 5; Table 2). Both the eastern GOM models and the Ricker models shown had their Bayesian p-values closer to 0.5 and higher percent overlaps of the marginal posterior distributions (Table 2).

The low and high recruitments were well replicated by models around optimal spatial scale (Fig. 5; Table 2). For the rest of the models, even though their performances of replicating all levels of recruitment were similar to the models of optimal spatial scales, these models could not replicate the low and high recruitments well (Fig. 5; Table 2). The p-values for low and high recruitment were below and above 0.5 at small spatial scales, gradually converged to 0.5 as spatial scales increased to the optimal size (Table 2). After exceeding the optimal spatial scale, the p-value was diverged from 0.5 again (Table 2). Similar results could be found for the

marginal posterior distributions: the observed and predicted distributions were barely overlapped at small spatial scales, but gradually overlapped when approaching optimal spatial scale (overlap coefficients close to 0.9); and diverged from each other again after exceeding the optimal spatial scale (Fig. 5; Table 2).

The western GOM, however, was an exception. None of the B-H models could predict the low and high recruitments well (Fig. 5; Table 2). For the low recruitments, at optimal spatial scales, the p-values were highest but still less than 0.1; and the overlap coefficients of marginal posterior distributions were highest but only around 0.3 (Fig. 5; Table 2). For the high recruitments, all the p-values are lower than 0.01 and overlap coefficients are lower than 0.15, suggesting a very poor model performance. The Ricker models could not well predict the low recruitments at all scales, but performed well for the high recruitments around optimal spatial scale.

Sensitivity of prior distribution

We compared the results of posterior predictive assessments of models using different prior distributions for parameters α , β , ν , and ε . The differences in overlap coefficients are mostly less than 0.1, suggesting that the posteriors are not sensitive to the prior distributions.

Stock-recruitment relationship

The Ricker and B-H SR relationships for the American lobster for the eastern and western GOM using data aggregated with different spatial scales were presented in Fig. 6. The

relationship differed greatly when data were grouped with different spatial scales (Fig. 6). When the spatial scale was too small, most of the data points were clustered at origin with large variations and therefore the recruitment was almost independent of spawning stock size (Fig. 6). When the spatial scale was too large, data points spread across different values of the spawning stock size but with large variations and the relationship could not be well determined (Fig. 6). The relationship between spawning stock size and recruitment was discovered at optimal spatial scale (Fig. 6). The data exhibited a clear Ricker type SR relationship for the east region (Fig. 6). For the west region, the data still revealed a Ricker type relationship but the recruitment declined at higher spawning stock size until the largest spawning stock size (Fig. 6).

404 *Discussion*

405 We estimated the SR relationship for American lobsters in the GOM using the same SR
406 data but grouped in different spatial scales. We demonstrated that the choice of spatial scale is
407 critical in quantifying the SR relationships. The spatial scale of data directly affected the
408 possibility of identifying the SR relationship, the estimation of SR parameters, the type of SR
409 relationships and the predictive abilities of the SR models. Therefore, the spatial scale has
410 significant influences on the SR data interpretations and the use of SR data for recruitment
411 predictions. The SR model parameter estimates are either negatively or concavely related to the
412 spatial scale of data used to build the model. This result implies that the spatial scale of data
413 used to estimate the SR relationship has systematic influences on the estimations of recruitment.
414 The parameter estimates of B-H models decreased with increasing spatial scales and were
415 lower at the median size spatial scales than other sizes for the Ricker model. The parameter α
416 is a location parameter in both the Ricker and B-H models, that is proportional to fecundity
417 (Quinn and Deriso 1999). A decrease in α for both models shifts the entire curve down,
418 which means that the estimated recruitments from the same amount of spawning stock size
419 decrease. Thus, size of the spatial scale has systematic influences on the prediction of stock
420 productivities. The β parameter measures the level of density dependence (Hilborn and
421 Walters 1992). A decrease in β decreases the rate of decrease of recruitment as spawning
422 stock size increases for the Ricker model and decreases the steepness at origin for the B-H

models. The decrease in β has more influences on the estimations of recruitment when the spawning stock size is low for the B-H models and high for the Ricker models. These results have significant implications for fisheries stock assessments since the SR relationship is one of the key functional relationships that determine the dynamics of the target population and reference point estimations (Hilborn and Walters 1992; Quinn and Deriso 1999). The trend in parameter estimates can cause bias in fisheries stock assessment though the bias can be inconsistent over years depending on the temporal stabilities of the mechanism that regulates the relationship.

Similar to the parameter estimates, the SR model fits and model performances in the posterior predictive assessment are convexly related to the spatial scale of data used to estimate the SR relationship. The best model was found at median spatial scale for both the eastern and western GOM. The fact that the parameter estimates and model fits are to some extent related to the spatial scale of data implies that the optimal spatial scale modeling the SR relationship does exist and is not an artifact.

The spatial scale of data could influence the possibility of discovering the SR relationship for American lobster in the inshore GOM. The SR relationships were detectable only at certain spatial scales. When the spatial scale was smaller than the optimal spatial scale, most of the recruitments were found at low spawning stock sizes with a few exceptions and the data tend to cluster at origin with large variations. The less the data are aggregated, the more the local

information is preserved. However, if the scale is smaller than the spatial scale at which the SR process operates, the information contains too much random noise that could mask the underlying relationships.

When the spatial scale is larger than the optimal spatial scale, recruitments were found at all levels of the spawning stock size but with large variations. If the data are largely aggregated, they are more a representation of the average regional or global conditions rather than the local dynamics. If the scale is larger than the spatial scale at which the SR process operates, the information is too general and the SR relationships could not be clearly revealed. This is especially applicable to the American lobsters in the inshore GOM area because their recruitments were found to be largely generated locally (Xue et al. 2008; Incze et al. 2010).

The 2002 to 2008 data used in this analysis reflect lobster stock conditions at historic high abundance (ASMFC 2009). Therefore, we may not have enough information to estimate SR relationships at low stock sizes (near origins) when the spatial scale of data is large (there are still data at low stock sizes when spatial scale of data is small). This is likely to affect the size and range of optimal spatial scale for SR analysis. If the data used in SR analysis include stock conditions at historic low abundance, the SR relationships might be better estimated at large spatial scales and the size of optimal spatial scale and range of spatial scales with good model fit might increase.

The differences of the SR model results for the eastern and western GOM seem to be related to the general circulation of the inshore GOM. For the eastern GOM, where the current is more steady and consistent, the range of the spatial scales with relatively good model fits is smaller (4-8 km). The relationship can only be found at specific spatial scales and the SR relationship is much more defined. In the western GOM, where the current is more variable and less constrained; the range of good model fits is wider (2-128 km). The spatial scales to discover the SR relationship is less specific and the relationship is less defined. The differences of the SR model results in the eastern and western GOM supported our hypothesis that the spatial scale of data used to build the model is related to the underlying mechanisms that result in the relationship. Similar results were shown in Incze et al. (2010) study of lobster larvae transport along the coastal GOM that the annual difference in postlarval days and abundances of competent postlarvae occurred primarily in the west region.

The performance of the Ricker model is superior to the B-H model for the data of optimal spatial scale and scales larger than 4 km for the eastern GOM and 16 km for the western GOM, indicating that density-dependent mechanisms are regulating the population dynamic of American lobster. One of the density-dependent mechanisms discovered for American lobster is cannibalism. This may play an important role in regulating the population size of American lobster due to the depletion of large predatory groundfish and record high lobster population size in recent years (ASMFC 2009; Oppenheim and Wahle 2013). This supports our results of

favoring Ricker type of SR relationship over B-H type. Our results showed that type of SR relationships varies by the spatial scale of data. Thus, misuse of the spatial scale of data to estimate the SR relationship could lead to misinterpretation of population dynamics.

We did not include any of the auxiliary variables while estimating the SR relationships for the American lobster in the coastal GOM. Many of the biotic (food, predation, etc.) and abiotic (temperature, current, etc.) variables were demonstrated to have impacts on the recruitment dynamics but the relative importance of these variables remains unclear (ASMFC 2009). In the coastal GOM, environmental and physical features differ between the east coast and the west due to variations in physical forces and inputs of multiple water masses. For example, summer bottom water temperatures are often warmer in the well-mixed EMCC and cooler in the well-stratified WMCC (Townsend 1991). The dissolved inorganic nutrients are higher in the EMCC but a majority of them were recycled into the WMCC resulting in a higher primary productivity in the western coastal GOM (Townsend 1991). Our analyses were done separately for the east and the west region. This should take into account some of the differences in the biotic and abiotic impacts along the coastal GOM. Since these impacts may also affect the spawning stock, they are likely to be confounded with the effect of spawning stock sizes when the spatial scale is appropriately defined.

Based on the posterior predictive assessment results, we show that there are significant discrepancies between recruitment observations and predictions when the spatial scale is too

small or too large, specifically for the low and high spawning stock sizes. "Essentially, all models are wrong, but some are useful" (Box and Draper 1987). Our results demonstrated that the SR model is not as useful when the spatial scale is misspecified. This result has significant implications to fisheries stock assessment, since the assessment results are usually more controversial when the spawning stock sizes are at the low or high end.

The spatial scale of fisheries management should be consistent with the spatial scale of ecological process. It would be possible to come up with a SR model that is useful for the whole GOM stock for American lobster since the optimal spatial scale for the eastern and western GOM does not differ greatly. However, the clearer relationship that we found for the east region might be masked if we model the GOM stock as a whole.

It is impossible (or too costly) to achieve a full mechanistic understanding of SR relationship by studying all the components and its interactions in the system, although the knowledge is essential for fully understanding the SR relationship. Without studying fundamental processes and the interaction between processes that result in the SR relationship, our approach is relatively simple, yet useful in demonstrating that SR relationship is process-related. Considering spatial scale of interactions of fundamental processes alone without including the processes themselves in the model could already increase the possibility of defining SR relationship. This study demonstrates that the influences of spatial scale of the data in estimating the SR relationship is significant and needs to be carefully considered,

especially for species with locally generated recruitment, complicated life history stages and populations structure, and complex interactions with their environments.

Acknowledgements

We thank R. Wahle and C. Bergeron for providing the recruitment data and R. Wahle for discovering a major data issue, A. Thomas for editing the manuscript, and three anonymous reviewers for valued comments that improved the manuscript.

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643 Table 1 Summary of posterior distributions for the stock-recruitment model parameters by
644 model type, spatial scale, and region.

			α			β		
Model	Region	Scale (km)	$\hat{R}_f$	Mean	95% CI	$\hat{R}_f$	Mean	95% CI
B-H	East	0.125	1.002	17657800	(841100,67190000)	1.002	11168550	(377900,42680000)
B-H	East	0.25	1.008	4174330	(180800,13570000)	1.008	2641645	(131300,8603000)
B-H	East	0.5	1.016	12895720	(430300,57190000)	1.016	8199449	(167400,35590000)
B-H	East	1	1.014	5663037	(207400,19890000)	1.014	3584460	(136300,12690000)
B-H	East	2	1.016	5258921	(188100,19100000)	1.016	3325061	(114400,11880000)
B-H	East	4	1.090	5859515	(78720,27850000)	1.090	3740566	(51410,17500000)
B-H	East	8	1.013	2292601	(232800,6446000)	1.013	1427700	(140500,4070000)
B-H	East	16	1.015	5272730	(181400,19970000)	1.015	3353335	(121700,12720000)
B-H	East	32	1.034	2336967	(78310,7608000)	1.034	1480368	(28090,4763000)
B-H	East	64	1.023	823661	(40390,2808000)	1.024	520997	(24460,1801000)
B-H	East	128	1.057	588102	(27280,1891000)	1.056	361240	(14640,1160000)
B-H	West	0.125	1.006	5701604	(229000,19880000)	1.006	2924222	(122200,10170000)
B-H	West	0.25	1.008	4626319	(260300,16340000)	1.008	2369218	(155000,8411000)
B-H	West	0.5	1.018	6590609	(256600,31090000)	1.019	3373607	(127200,16160000)
B-H	West	1	1.005	2365896	(184200,7535000)	1.005	1213146	(91100,3872000)
B-H	West	2	1.012	2299235	(124100,6103000)	1.012	1184195	(66360,3129000)
B-H	West	4	1.008	2082435	(133900,6534000)	1.008	1067173	(68350,3295000)
B-H	West	8	1.058	1058384	(70870,3481000)	1.058	544013	(37270,1758000)
B-H	West	16	1.040	1158222	(64500,3969000)	1.040	601667	(32300,2083000)
B-H	West	32	1.003	1005963	(61050,3185000)	1.003	524957	(32900,1656000)
B-H	West	64	1.009	600675	(91460,1474000)	1.009	312582	(37870,769500)
B-H	West	128	1.051	824013	(85090,1668000)	1.051	440276	(43130,893200)
Ricker	East	0.125	1.001	109.40	(63.62,161.7)	1.001	6.14	(4.276,7.862)
Ricker	East	0.25	1.002	63.05	(42.7,86.2)	1.002	5.22	(3.853,6.541)
Ricker	East	0.5	1.001	54.72	(37.27,76.48)	1.001	4.96	(3.519,6.222)
Ricker	East	1	1.001	49.30	(33.29,67.01)	1.002	4.65	(3.559,5.846)
Ricker	East	2	1.001	49.93	(31.07,70.26)	1.001	5.06	(3.804,6.308)
Ricker	East	4	1.001	79.42	(46.47,115.3)	1.001	6.20	(4.629,7.737)
Ricker	East	8	1.006	57.60	(33.43,82.01)	1.010	5.52	(3.694,7.079)
Ricker	East	16	1.001	52.74	(31.34,78.06)	1.001	5.67	(4.003,7.203)
Ricker	East	32	1.004	85.88	(24.66,155.1)	1.003	6.18	(4.348,8.023)
Ricker	East	64	1.005	130.96	(3.829,356.2)	1.013	5.62	(2.53,8.434)
Ricker	East	128	1.004	127.61	(4.735,350.7)	1.003	5.63	(2.422,8.447)
Ricker	West	0.125	1.001	66.57	(52.88,79.38)	1.002	4.73	(3.676,5.748)
Ricker	West	0.25	1.001	68.63	(56.35,81.39)	1.001	4.72	(3.717,5.747)
Ricker	West	0.5	1.002	57.09	(46.07,67.89)	1.001	4.76	(3.748,5.744)
Ricker	West	1	1.001	42.44	(34.2,51.44)	1.001	4.15	(3.286,5.061)
Ricker	West	2	1.002	33.61	(26.6,41.08)	1.002	3.99	(3.169,4.869)
Ricker	West	4	1.001	35.47	(25.74,44.95)	1.001	4.42	(3.289,5.44)
Ricker	West	8	1.002	36.12	(24.21,51.3)	1.002	4.77	(3.573,5.996)
Ricker	West	16	1.001	45.86	(22.63,72.39)	1.001	5.49	(3.867,7.308)
Ricker	West	32	1.001	43.49	(14.86,82.35)	1.001	4.72	(2.474,6.792)
Ricker	West	64	1.005	39.76	(7.761,88.56)	1.007	3.80	(1.434,5.9)
Ricker	West	128	1.008	100.11	(4.455,278.7)	1.021	5.44	(1.791,8.989)

645

Table 2 Overlap coefficients (OV) and Bayesian p-values (p) for all, low-level (<25th percentile), and high-level (>75th percentile) recruitments by model type, spatial scale, and region.

Region	Scale	B-H Model						Ricker Model					
		All R		Low R		High R		All R		Low R		High R	
		OV	p	OV	p	OV	p	OV	p	OV	p	OV	p
East	0.125	0.95	0.51	0.76	0.33	0.11	0.01	0.96	0.51	0.30	0.91	0.23	0.05
East	0.25	0.93	0.54	0.72	0.31	0.12	0.01	0.95	0.53	0.02	0.00	0.04	1.00
East	0.5	0.94	0.53	0.81	0.39	0.10	0.01	0.98	0.51	0.10	0.99	0.04	0.00
East	1	0.93	0.53	0.78	0.33	0.13	0.01	0.95	0.52	0.20	0.96	0.01	1.00
East	2	0.94	0.52	0.78	0.36	0.11	0.01	0.96	0.52	0.21	0.96	0.73	0.61
East	4	0.93	0.54	0.96	0.54	0.63	0.25	0.94	0.54	0.92	0.57	0.80	0.36
East	8	0.97	0.50	0.96	0.47	0.93	0.46	0.96	0.53	0.97	0.48	0.94	0.52
East	16	0.97	0.51	0.72	0.30	0.18	0.02	0.98	0.50	0.93	0.53	0.86	0.58
East	32	0.94	0.53	0.79	0.36	0.21	0.03	0.95	0.52	0.83	0.41	0.54	0.20
East	64	0.96	0.51	0.76	0.33	0.20	0.03	0.94	0.53	0.85	0.40	0.37	0.11
East	128	0.94	0.52	0.75	0.33	0.24	0.05	0.95	0.54	0.79	0.36	0.33	0.07
West	0.125	0.91	0.45	0.25	0.05	0.06	0.01	0.05	0.01	0.00	0.00	0.10	0.99
West	0.25	0.95	0.51	0.25	0.06	0.07	0.01	0.95	0.52	0.00	0.00	0.31	0.93
West	0.5	0.96	0.50	0.26	0.06	0.07	0.00	0.96	0.48	0.00	0.00	0.29	0.93
West	1	0.96	0.53	0.29	0.07	0.09	0.01	0.95	0.49	0.05	0.00	0.32	0.92
West	2	0.96	0.50	0.29	0.06	0.08	0.01	0.95	0.53	0.13	0.02	0.55	0.79
West	4	0.97	0.49	0.26	0.06	0.07	0.00	0.96	0.48	0.21	0.03	0.82	0.61
West	8	0.94	0.53	0.26	0.06	0.09	0.01	0.95	0.53	0.25	0.04	0.88	0.42
West	16	0.96	0.53	0.25	0.05	0.12	0.02	0.94	0.52	0.17	0.03	0.71	0.31
West	32	0.95	0.52	0.25	0.06	0.15	0.02	0.96	0.50	0.18	0.03	0.65	0.25
West	64	0.96	0.52	0.26	0.06	0.10	0.01	0.97	0.51	0.38	0.10	0.26	0.05
West	128	0.94	0.53	0.28	0.06	0.13	0.02	0.95	0.50	0.29	0.07	0.21	0.04

Fig. captions

Fig. 1 Summer schematic diagram of EMCC and WMCC for the upper 40m in the GOM. The letters A-G designate Lobster Management Zones.

Fig. 2 Estimated spawning stock size (# per 792 m²) summarized using smallest (0.125km, a), median (0.8km, b), and largest (128km, c) spatial scales and recruitment (# per m²) based on the DMR settlement survey along the coastal GOM for year 2008. The letters A-G designate Lobster Management Zones.

Fig. 3 Box plots of square-root-transformed α and β parameter estimates of the stock-recruitment models by model type, spatial scale, and region.

Fig. 4 Box plots of deviances of the stock-recruitment models by model type, spatial scale, and region. Black bar = mode.

Fig. 5 Marginal posterior densities for observed (black line) and replicated (gray shade) discrepancy measures for all levels (top), lower levels (<25th percentile), and higher levels (>75th percentile) of recruitments by model type and spatial scale for the eastern (a) and western (b) GOM.

Fig. 6 Stock-recruitment relationships with observations (hollowed dots) and marginal posterior modes (solid triangles) by model type and spatial scale for the eastern (a) and western (b) GOM. Black lines are the models of marginal posterior mode and red lines are the models of 500 parameter sets randomly drawn from the marginal posterior

671 distributions.

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672 Fig. 1

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675 Fig. 2

676 (a)

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678 (b)

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680 (c)

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688 Fig. 5

689 (a)

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692 (b)

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695 Fig. 6

696 (a)

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700 (b)

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